

A BUCCULATRICID GALL MAKER AND ITS HYPERMETAMORPHOSIS

BY JAMES G. NEEDHAM

I have a pocket-knife that whittles, and once when I was out in a South Florida wilderness in December, I came upon a patch of wild sunflowers with knot-like swellings in their stems. I set my knife to whittling, and soon found that the swellings had very hard walls and were hollow inside. They were galls; and lying inside each gall was a very curious larva. It was evidently a moth larva of some sort, but it had a very small head, a nearly moniliform body (by reason of deep and wide constrictions between the body segments), no hair or spines or setæ on its dry, tough skin, and no prolegs. It did not creep, but lay on its side with the front end thrown back in a J-shaped hook, the head at the tip of the hook. It spun no silk, not even enough to hold back the pellets of frass. It lay among these dry pellets and tumbled around with them when the gall was shaken. When the gall was opened and inverted, the pellets fell out in a shower, like that from an up-tipped pepper box.

Specimens of the larva were sent to Dr. W. T. M. Forbes and Mr. H. W. Capps, and neither would venture a determination nor even a reference to any Lepidopterous family. They both suggested that I rear the larvæ and send in some adult moths. So that is what I did; and on the doing of it (and certain related other things) I now herewith make report.

The plant is a native annual sunflower, *Helianthus agrestis* Polard (*H. curtissii* Fernald). On the rich soil in which I found it, it grows head-high, on wand-like stems. Crowded together in close ranks, the stems rise unbranched to shoulder height; where not crowded they branch extensively at lower levels. I found them in nearly pure stands in long patches of an acre or less, these patches in the edge of low places in the flatwoods, in spots too wet for saw palmetto and for most grasses, and too dry for saw-grass and for marsh fleabane (*P. lucheæ*), but with the two

latter generally near at hand. All that I saw were within a mile or two of salt water, between Sarasota and Englewood.

The gall is a thickening of the walls of the stem, about an inch long and four-fifths as wide, and with a large oval cavity inside. It varies in form from oblong to almost round. It tapers a little more abruptly to the stem at the upper end. Its surface is generally bare and somewhat uneven. The outer layer of its walls is filled with rosin, and is very hard, especially on the upper side. Its cavity is normally centrally located in the axis of the stem, but sometimes it is on one side, where it causes a jog in the stem. In such a case the rosin is deposited only on the bulging side, the opposite side remaining soft as elsewhere on the normal stem.

The walls of the gall vary in thickness and consistency. Generally when old and dry there is an inner brittle layer formed by the drying up of the pabulum tissue that earlier feeds the larva; and between this and the very hard resin-filled outer defense layer there remains some softer parenchyma. Certain inquiline (to be noted later) burrow in this softer tissue. Elsewhere in the plant the stem is filled with pith.

Galls occur singly on the stems; very rarely two, and when two, one or both are imperfectly formed. They are generally located somewhat below mid-height of the plant. Often growth continues above the gall, not in a single normal stem, but in several weaker branches that may, however, bear perfectly normal heads of flowers, at the general level above. A few belated flowers on over-shaded and dwarfed stems were still present in December. The blossoming heads are very pretty, with their bright yellow rays, and disc flowers of deep violet.

The gall-making larvæ in the winter season are full-grown and full fed, awaiting the warmer weather of early spring for transformation. Placed on a flat surface they are quite incapable of locomotion, and lie always in a lateral position. Touched at any point on the body, they respond with a sudden lashing motion that may be repeated several times before coming to rest again. The J-shaped hook at the front may be a position assumed in preparation for attack by an enemy, for dead specimens lie straight and fully extended.

The length of grown larvæ varies from 10 to 12 mm. Dorsal

and ventral surfaces are similar in appearance, both being a little flattened and narrowed toward each end.

Although the larva, if undisturbed, lies inactive within the gall all winter long, important changes are going on inside it. It is about to resume a more normal lepidopterous larval form, preparatory to transformation to the pupal stage. What was my surprise, on opening a gall in early March of 1946, to find a cast-off larval skin of the form above described, and a living larva of quite a different form beside it. The new larva was cylindric in body. It crept about on regular caterpillar prolegs. Its body bristled with setæ. Its head was of the proper size for a normal lepidopteran, and it could spin silk!

Here was a non-feeding instar, interpolated between larval and pupal stages: a clear case of hypermetamorphosis.

The larva in this non-feeding stage has strong mandibles, and it gnaws a hole through the wall of the gall to the outside. Then it returns and casts off a very thin transparent skin; thin, except on the brown head, where the strong jaw muscles require solid support for their gnawing. Behind the head the skin is soft and papery. It gets compacted into a little bunch in which black dots mark the bases of the body setæ. The duration of this stage is very short, probably less than a week.

The pupa is of ordinary lepidopterous form. The adult is a little bucculatricid, whitish moth¹ (length about 6 mm.) without any brilliance of coloration; creamy white with just enough touches of tan and brown to make its rough surface and frayed-out wing margins look as lifeless as a bit of bark torn from a broken sunflower stem by the wind.

I had my troubles rearing this larva. I collected galls by the score, repeatedly, through two winter seasons at Sarasota, Florida. I opened galls by the dozen looking for signs of development, and finding none. I kept them under varied conditions of temperature, moisture, and exposure to sun, rain, and wind, opening some of them weekly or oftener only to find in the end that none of these measures was of any effect. My troubles were all due to enemies: to mordellid beetle larvæ: mites, and ants.

The final rearing of the moths came by partial successes. On

¹ Now in the hands of Dr. Annette Braun for description.

the first of February, 1945, I found a gall that had a very active larva inside it. I put back the chip removed in opening the gall, fastened it securely, put it in a tray, covered the tray with a close-fitting glass plate, set it in a South window where it was exposed to sunshine in a warm room. Next day there appeared a white cocoon on the smooth inner edge of the rim of the tray. It had been spun during the night; a beautiful cocoon, close-woven to fit the body of the larva on the inside, overspread with a dainty outer covering, raised in parallel ridges of exquisite weaving.

This pearly white, finely wrought, ribbed cocoon cover gave the first hint as to the systematic position of the species. Well-known apple pests of the genus *Bucculatrix* make similar ribbed cocoons. This specimen, however, I was unable to rear. The ants got it; little yellow ants so small that they could go through a needle's eye in double columns; and there ended that season.

I returned to Sarasota in January 1946 to finish the job. Other enemies than ants had plagued my rearing jars during two preceding winter seasons, two kinds that were much harder to deal with than ants. Mordellid beetle larvæ and mites were thwarting my attempts at rearing the gallmaker; and I had first to study their habits.

Mordellid beetle larvæ are well-known pith borers; generally accounted herbivorous, but hitherto only vaguely suspected to be partly carnivorous in their feeding habits. They are regular residents in the stems of this species of *Helianthus*. Hardly a stalk in a whole field was without their burrows, running up and down through the pith. The burrows vary greatly in diameter as the larvæ do in size.

Larvæ may be found by chipping off a bit of the stem wall, but when so exposed, they make haste to get under the next chip. One of them may be chased to the end of its burrow by removing successive chips.

The form of the larva is roughly cylindric, with great humps upon the back of several abdominal segments that look and function like prolegs. Travel up or down the burrow is done by pushing or pulling one end of the body forward while holding fast with the other.

The larva is superbly fitted for its tube-dwelling life, and un-

fitted for any other. Dumped out of its burrow and lying on a plane surface, it is helpless. It can only lie on its side and squirm and roll over. Other animals have been termed "side winders" but this one surely best deserves that name. The manner in which it uses its locomotor appendages may be seen in detail by putting an uninjured larva in a glass tube of proper diameter of bore (methods used by Anna May French in studying the larva of *Mordellistina nigricans* Melsh.: see *Psyche*, 44: 34, 1933).

In November and early December, when nearly every gall contains a living larva of the gall-maker and while the *Helianthus* stems are still green, the beetle larvæ are to be found in the pith below the galls. Later the beetle larvæ extend their burrows upward and enter the galls. They pass by the frass-filled conical pit at the center of the gall base. They seek out the softer parenchyma of the middle layer of the side wall and often burrow through it and beyond it before penetrating the inner brittle layer that is the gall-maker's last wall of defense. There is abundant evidence that they enter and kill the moth larva.

A sample count of the contents of 80 galls, collected near Woodmere on February 19, 1946, will show this. Inside 80 of these apparently normal galls were found:

- 20 living bucculatricid larvæ, with no signs of mordellids present.
- 11 dead bucculatricid larvæ.
- 30 empty, with connecting mordellid burrows.
- 8 living mordellid larvæ with dead bucculatricid larvæ alongside them.
- 1 living mordellid pupa.
- 10 aborted galls, with bulging inner-gall tissues and no larvæ of either species present.

Often, in an empty gall with a connecting mordellid burrow, there would be a little tuft of hard fibro-vascular bundles of *Helianthus*, lying loose in the bottom of the gall. I guess that these were from the gall wall (for they seemed to be of special hardness), and were stripped of their surrounding softer pith cells by the entering larva and pushed inside.

Probably the predator leaves by the way it enters, and goes

back down the stem to pupate, for mordellid pupæ generally were found in burrows lower down on the stems, often near the ground level.

The mites (*Pediculoides ventricosus* Newport) are even more destructive. They follow the mordellids in season, and seem to be more or less dependent on the beetle larvæ for gaining access to the tightly closed galls. I found mites only in galls that had an opening to the outside.

After slicing the side of a gall off smoothly and finding a healthy moth larva inside, I tried many times by various means to fasten the piece back in place securely, but never succeeded in keeping the mites out. I lost every one. Sometimes when finally re-examined there would be only a few mites present, sometimes scores of them. But even if only one or two, the moth larva would be dead or dying. It probably exhausts its store of energy by continuous repetition of its extremely vigorous avoidance reaction. Where touched ever so lightly it lashes its body and springs away.

These very little 8-legged mites (about length 0.5 mm.) are well-known enemies of various lepidopterous larvæ. When a mite begins sucking up the juices of the moth larva, its abdomen quickly swells up to spherical form, and takes on a shining honey-yellow color. With its abdomen swollen to full rotundity, it presents a miniature parallel, in appearance, to the storage-individual honey-ant of Texas. With many mites sucking together, the moth larva quickly shrivels to an empty, crumpled skin.

I finally succeeded in rearing a series of the bucculatricid moths by collecting selectively in the field several hundred apparently sound galls, cutting off the stem close to the gall and examining the cut end to see that no mordellid burrow had penetrated it. Then I divided the sound galls into lots, and put them in ant-proof cages. I placed some outdoors, one exposed to rain and sun, one under shelter and one in the shade; kept some indoors, in cool rooms and warm, in moist air and in dry. I soon saw that the larvæ in several of the cages were coming out to spin, and before the first of March, when I had to leave Sarasota, moths had emerged in all the cages.

The larvæ spurned every sort of pupation shelter that I offered

them, and came out into the open and settled down in the most exposed places available. Each larva spun for itself the ribbed, silken coverlet and then the tight-fitting cocoon closely wrapped around its body underneath.

OTHER INHABITANTS OF THE GALLS: INQUILINES, ETC.

There is a little moth larva that lives in a burrow of its own in the softer middle tissue of the wall of the gall. This larva is less than half an inch long, of the ordinary lepidopterous form (with setæ and prolegs); pale yellowish, with a mid-dorsal line of red, and a row of diffuse reddish spots along each side on the lateral prominences of the segments. I did not rear it. Only two specimens were encountered and both were damaged in opening the galls. The burrows entered from pith below the gall, and this species is probably to be ranked as a stem borer.

Hippopsis lemniscata (F.). A small collection of galls with stems attached yielded (on dissection) a score or more of larvæ of this curious little cerambycid (long-horn) beetle. Some of these came from the softer tissues in the walls of the galls.

Toxotropis submetallicus Schaeffer. Of this small fungus weevil (Curculionidæ) hitherto reported from Texas and known also (to Dr. Henry Dietrich) from Mississippi, many specimens emerged in one of my rearing jars. Aborted galls often contain growths of fungi, and this beetle may have developed in these.

A minute tenebrionid (darkling beetle) larva occurred sparingly in the pith of both stem and gall. Mr. R. A. St. George reported on it as being "close to *Aphanotus*." It has a very slender, strictly cylindric body, smooth on the surface, like a "wireworm," with a pair of sharp upcurving hooks on the tip of its tail end.

Ormiscus sp.? A single larva of this genus (family Anthribidæ) was found in dissecting a gall; the genus, reported heretofore as "removed from dead twigs."

Schizoprynus sp.? This braconid parasite emerged in one of my rearing jars on April 21, 1945, among the late emergences from that jar. When sent to Dr. C. F. W. Muesebeck, he reported the above name, and commented: "This genus is wholly unworked. Specific distinctions have not been established.

Therefore we have as yet no basis for specific identification." I can make no suggestion as to whether the Bucculatricid larva or some other resident species is its host.

Such is the gall that set my knife to whittling, and such the moth that causes the gall to grow, and to provide shelter for its own curious larvæ and for other insects besides: for its pith-dwelling mordellid neighbors, that come up the stalk from below and become its enemies; for hordes of devastating mites, seeking entrance at every crevice; for the guests that take up their abode in the outer wall of the gall and live apart; and for at least one species of parasite.

Not least in interest concerning this little tatterdemalion moth is its way of entering upon the pupal stage. As a larva it has lived secure inside the gall with all its wants supplied. And in form it has departed far from the ancestral pattern. It must get back on the beaten track. Before it can enter the pupal stage it must regain caterpillar form and functions. This requires a making-over into the normal, with a restoration of jaws for hard chewing and silk for spinning during a non-feeding stage. This is *hypermetamorphosis*: an added change of form. There is no other way it can become a pupa and then a moth than the old way by which ancestral moths developed. Herein appears the force and the meaning of biological tradition.

And when this restoration of form and of primeval powers has been accomplished, the larva builds its pupal shelter out of gossamer threads of pearly whiteness, weaving its coverlet with marvelous artistry.